MASSACHUSETTS
AGRICULTURAL EXPERIMENT STATION

Bulletin No. 350 May, 1938

Tomato Leaf Mold as Influenced by Environment

By E. F. Guba

Knowledge of the life history of the tomato leaf mold fungus and the factors which favor infection is fundamental to an understanding of control measures. This bulletin deals with the various environmental factors which influence the development of the fungus and the infection of the tomato plant in the greenhouse.

MASSACHUSETTS STATE COLLEGE
AMHERST, MASS.

TOMATO LEAF MOLD AS INFLUENCED BY ENVIRONMENT

By E. F. Guba, Research Professor of Botany

INTRODUCTION

Tomato leaf mold, caused by the fungus *Cladosporium fulvum* Cke., has been the subject of numerous investigations, particularly in England, Germany, and the United States. For several years, the disease has been studied in Massachusetts in an effort to further knowledge of its control in the greenhouse. More recently, the work has been confined entirely to the development of suitable resistant varieties. It is the purpose of this paper to offer the results of studies dealing with the relation of environmental factors to the development and parasitism of the causal fungus, together with a comprehensive review of the pertinent literature. In view of the investigations now being pursued in different countries on the genetics of the tomato in relation to the parasite, the publication of these studies would appear opportune.

THE DISEASE

The reduction in yield and quality of tomatoes under glass as a result of the destruction of the foliage by the leaf mold fungus is familiar to every grower. The planting started late in the winter, which is designated the spring crop, usually shows signs of disease in the month of May. The disease gradually becomes epidemic as summer weather approaches. The second planting, started in July and August and designated the fall crop, is very seriously affected from the beginning, and usually by November, especially if the heating has been poorly managed, the foliage is destroyed except for a tuft of uninfected leaves on the tops of the trellised plants. The loss of foliage retards and checks the growth of fruit and reduces the volume and quality of the crop. This loss is much greater in the fall than in the spring. Usually, because of late incidence of the disease in the spring season of cropping, no real or apparent loss in yield is admitted.

The leaf mold fungus also causes a black stem-end rot of tomatoes. The rot results from the invasion of the fruit at the stem end by the mycelium of the fungus in consequence of spore infection of the blossom (9, 10, 13). When the blossoms and subsequently the ovaries are infected, the young fruits fail to develop and fall from the plants. The invasion of the more mature fruits with subsequent stem-end decay also makes possible the infection of the seed and the transmission of the fungus with the seed. This black stem-end rot is rare in Massachusetts greenhouses.

Seasonal climatic variations appear to govern the prevalence of the disease in greenhouses. In England the disease is most severe from May to August and only of slight importance from November to March (27, 31). In New Zealand there is no leaf mold for the first three to four months of growing, but with the occurrence of warm, wet weather in October and November, the disease may considerably damage the crop (6). In Massachusetts the disease is not restricted to greenhouse tomatoes. Its occurrence has been noted in epidemic form in outdoor plantings adjacent to greenhouses cropped to tomatoes and in stagnant areas associated particularly with uneven topography of the land and poor atmospheric drainage. The disease is of frequent occurrence in hotbed and cold-

frame plantings here and elsewhere (23, 33), and in some years may appear as early as January on seedlings and plants for the first or spring planting in the greenhouse (23). It is reported to appear first and most seriously in the south and west sides, corresponding to the hottest parts of the greenhouse, and in east and west houses; and least in the north and east sides and in north and south houses (1, 7, 40). The lowest leaves become infected first. The occurrence and the epidemic development of the disease in definite situations and during definite seasons of the year, suggest the close association of the disease with particular environmental factors of light, temperature, and humidity.

THE FUNGUS

Careful life-history studies have never revealed more than the conidial stage of the fungus as it occurs on tomato foliage. Sclerotial bodies of the fungus have been noted in infected tomato seed (10), on corn kernels in pure culture (13), and as an overwintering stage which on the advent of spring produced conidia (3); but fruiting bodies of a perfect stage have never been observed (11). In the light of extensive observations and the unsuccessful efforts of other investigators to obtain the perfect stage, it appears that the fungus has never had the ability to produce pleomorphic spores. This fact has simplified the means possessed by the fungus for its survival and spread.

The conidia possess extraordinary resistance to extremes of environmental conditions which assures the occurrence of the disease from one year to the next. Plants have been infected with conidia from a leaf dried between blotting paper for six months, and after a period of one year some conidia were still viable (13). Spores exposed to a dry atmosphere for eight months were for the most part capable of germination; after ten months, only a small percentage was viable; and after twelve months none were viable (11). New spores have been observed to germinate in four hours; spores eight months old, in 24 hours. After being outdoors in a dry condition from January 4 to May 1, during which time the lowest recorded temperature was —4° F., spores germinated readily (32). Spores from overwintered leaves produce infection the following spring after passing severe winters on glasshouse structures and in the soil (27, 29).

The writer's experiments have shown that a large percentage of the conidia exposed under various temperature conditions was still viable after nine months. The death of the spores increases slowly with age. The fungus readily survives gaps between tomato crops in the greenhouse, and the source of the spores may be from the greenhouse itself or from the field.

The fungus has been grown on filter paper (13); on partially dead corn leaves; on detached tomato leaves (32); and on a decoction of tomato and tobacco leaves (11). This would suggest that the fungus exists on dead substrata in the absence of and apart from its susceptible living host, and that it is to be regarded as a facultative parasite.

The conidia of the fungus are disseminated chiefly by currents of air. The spores are easily dislodged from the leaves when the vines are disturbed in pruning and harvesting and by drafts of air, and are readily spread in the air throughout the greenhouse planting. Tapping or shaking the plants to assist in pollination of the blossoms, which is a usual and desirable cultural practice, dislodges clouds of spores into the air. The workers also collect spores on their clothing as they walk between the rows of plants and thus readily disseminate the fungus.

RELATION OF ENVIRONMENTAL FACTORS TO SPORE GERMINATION AND GROWTH

Relative Humidity

Makemson (13) reported good fungus growth at 97% relative humidity, excellent at 88%, poor at 75%, and none at 60%, on artificially inoculated plants under jars. In his experiments, these humidity values were maintained fairly well with sulfuric acid, but they were regarded as somewhat low due to the inaccuracies of the polymeter used. The optimum humidity for the fungus and the tomato plant were reported to be the same. Newhall (15, 16, 17) could not germinate the conidia below 96% relative humidity at room temperature, and reported that germination was best at 98 and 99%. In contrast, Rippel (22) found that at 40° and 68° F. spore germination was 100% at 95 and 100% relative humidity; 50 and 60% at 90% relative humidity, and none at 85%. He regarded the fungus as a xerophyte, and asserted that the spores were unable to germinate unless a positive moisture differential existed between the relative humidity of the air and the minimum hydration index of the spore, which he asserted to be 85% relative humidity. At an atmospheric relative humidity of 100%, the moisture available for swelling spores is maximum and offers the best chances for germination.

Studies were undertaken by the writer in an effort to obtain further convincing evidence. Conidia of the fungus were obtained from infected leaves and applied to glass slides with a camel's-hair brush. The tests were conducted under bell jars, and variations in the relative humidity of the air were obtained with different concentrations of sulfuric acid. Small tomato plants were placed with the slides under each jar. A Mason hygrometer was suspended in each jar and the entire equipment was incubated in controlled air temperature chambers. Readings of relative humidity were made frequently during the experiment. The conidia were incubated for periods of 24, 48, and 72 hours, and were thereafter placed in moist Petri dishes to make certain of their viability. The temperatures used ranged from 68°-72° F. In all the tests in which the spores were exposed to a relative humidity of 100% excellent germination occurred.

A film or drop of water is not required for germination, although the spores germinate excellently in this medium. In 20 tests in which the conidia were exposed to relative humidity values between 83 and 89% inclusive, there was no germination. In one series of experiments no germination occurred within a range of values of 90-95%. Germination was noted at 96% relative humidity and it was better at higher values up to 100% at temperatures of 68°-72° F. In another series of experiments in which temperatures of 78°-86° F. prevailed, germination occurred at 95 and 96% relative humidity; it was very poor at 94%; and there was only a trace at 90 and 92%. In other instances no germination was noted at 90%. Under the conditions of these experiments and under optimum temperature conditions for germination, a relative humidity of at least 95% is required for spore germination.

In other experiments, the spores of the fungus were applied to selected areas on the lower leaf surfaces of potted tomato plants. These plants were covered with open-topped bell jars plugged with cotton, in each of which was suspended a Mason hygrometer. The entire assembly was subjected to controlled temperatures. The relative humidity values were obtained with sulfuric acid. After an incubation of 72 and 144 hours, pieces of epidermis from the inoculated areas

of the leaves were removed and examined under the microscope for spore germination, and subsequently placed in moist Petri dishes to determine spore viability. The results in Table 1 show that under optimum temperature conditions spore germination is extremely rare at relative humidity values of 90-95%. Values above 94% are favorable to germination, and a value of 100% is optimum. These results are closely in line with the findings of Newhall (15, 16, 17).

TABLE 1. RELATION OF RELATIVE HUMIDITY TO SPORE GERMINATION ON LEAVES OF TOMATO

Temperature °F.	Relative Humidity Percent	Spore Germination 72 Hours	Spore Germination 144 Hours	Viability
78–80	100	Good	Good	Good
78–80	90–95	Rare*	Rare*	Excellent
77–80	90–95	Rare*	Rare*	Excellent
78–80	85–90	None	None	Excellent
78–80	71–80	None	None	Good
78–80	56–71	None	None	Excellent
61–63	100	Good	Good	Good
62–64	96–99	Fair†	Fair	Excellent
62–64	94–98	Fair†	Fair	Excellent
61–62	94	Rare*	Rare*	Excellent
61–63	82–88	None	None	Excellent
61–63	72–82	None	None	Good

*Short germ tubes
†Growth of germ tubes retarded

Temperature

The temperature relations of the fungus have received considerable study. Gardner (10) found that the minimum and maximum temperatures for growth and sporulation on potato dextrose agar are 35.6° and 95° F. respectively, and the optimum 68°-75.2° F. Caldis and Coons (5) reported no growth on Shives' dextrose agar at 50° and 86°-89° F. Makemson (13) asserted the minimum, optimum, and maximum temperatures for development of the fungus on the plant to be 48.2°, 68°-77°, and 86° F. respectively. Different opinions are reported concerning the relation of temperature to spore germination (Table 2). On the basis of the writer's study, spore germination occurred over a range of 40°-94° F. with the optimum at 75°-78° F. (Fig. 1). The optimum is considered the same as the most favorable day temperature for growing tomatoes under glass. Between 40° and 61° F. germination and the growth rate are slow. As the temperature increases from 79° to 94° F. the growth rate decreases rapidly.

Hasper (11) found that the spores are killed when frozen in ice at 2° F. for 7 days, but when left for the same period at a minimum temperature of about 8° F., a large part of the spores germinated. Spores sown in water at temperatures between 122° and 140° F. were killed. Dry air temperatures of 156°-158° F. for 4 hours were lethal, but after 3 hours some germination occurred. Exposure of spores to free winter weather for 3 months destroyed them. According to Spangler

Table 2.--Temperatures at which Spores of *Cladosporium fulvum* Germinate

Authority	Temperature at which spores germinate		
	Minimum °F.	Optimum °F.	Maximum °F.
Bewley (4)		71 –77	90
Hasper (11)	32–33.8	68 –79.7	87.8–91.4
Makemson (13)	46.4	64.4–75.2	86
Small (26, 27, 30)	38	72 –77	89
Williams (39)		79 –81	90
Newhall and Wilson (15)	42.8		84.2
Alexander (2)		63 –70	90
Wollenweber (41)		68 –77	93.2
Gardner (10)	41	68 –77	95
Guba	40	75 –78	94

(32) winter weather from January 4 to May 1 at which a low temperature of —4° F. was reached did not affect the viability of the conidia. Judging from the epidemic occurrence of the disease from year to year, it seems that in Massachusetts, winter weather conditions have no adverse influence upon the fungus. Knowledge of the higher thermal death point would appear to have some practical application since high temperatures were advised in England in an effort to control the disease. Wright (42) and Thompson (35) advocated raising the greenhouse temperature to 110°-120° F. every second day for a week, and it is further noted

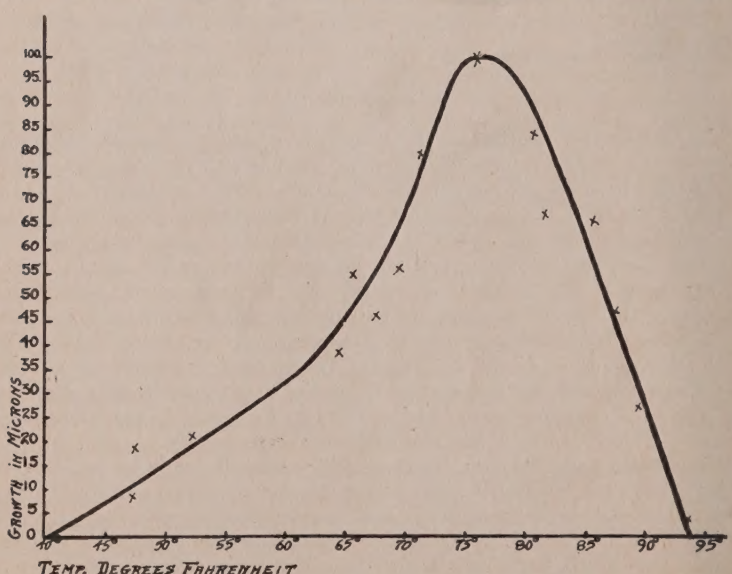


Figure 1. Relation of Temperature to Growth of Germ Tubes after 48 Hours Incubation

that a temperature of 100° F. for 2-3 hours at intervals of a week was offered as a valuable control measure (1); but Small (30) reported that the spores on diseased plants could not be killed by maintaining temperatures above 100° F. for several hours each day, nor when the maximum temperatures were made to reach 110°-130° F.

In the writer's studies on this question, the conidia were applied to glass slides with a camel's-hair brush and incubated in a dry atmosphere at temperatures of 100°-115° F. for different periods of time. After the designated period of incubation, the slides were placed in moist Petri dishes at optimum temperatures for germination to determine the viability of the conidia. It was shown that exposure for 2 hours to a temperature of 115°-116° F. destroyed their viability. At slightly lower temperatures, longer periods of exposure were required to kill the conidia (Table 3). At a temperature of 104° F. this was accomplished within 20-22 hours. From the results in Table 3, it is evident that a range of temperatures from 104°-115° F. is fatal directly in proportion to the period of incubation, when free spores are exposed.

TABLE 3.--PERCENTAGE OF GERMINATION OF SPORES OF *Cladosporium fulvum* AT DIFFERENT TEMPERATURES AND PERIODS OF EXPOSURE

Temperature °F.	Percentage of Germination After Exposure of —										
	2 Hr.	4 Hr.	6 Hr.	8 Hr.	10 Hr.	12 Hr.	14 Hr.	16 Hr.	18 Hr.	20 Hr.	22 Hr.
115.........	–										
110–112.......	†	Tr.	–								
109–110.......	75	Tr.	–								
107–108.......	75	14	4	–							
105–106.......				25	10	6	2	–			
104.........					80	48	25	11	4	Tr.	–

†Germination
–No germination
Tr. Trace of germination

Subsequently, small diseased potted plants were exposed to temperatures of 108°-110° F. for different lengths of time. Germination was not affected by an exposure of 2 hours, but was reduced about 75% by an exposure of 4 hours, and about 90% by an exposure of 6 hours. Injury to the foliage, especially tender and diseased areas, occurred in each instance and increased in severity with the duration of exposure. Further experiments were conducted in a greenhouse of 1,000 square feet with matured tomato plants on which infection was epidemic. On one occasion temperatures ranging from 105°-110° F. were maintained for 2 hours; on another, 118°-123° F. for 3 hours. The plants were injured by the latter treatment but spore germination was not appreciably affected.

Light

Light has a retarding influence on the growth of the spore germ tube, and is unfavorable to the best growth of the fungus in culture (13). According to Volk (36), bright light causes a rich growth of spores on the leaves, and darkness

favors rapid vegetative growth. Hasper (11) noted that several hours exposure to direct sunlight is lethal to the spores.

The influence of light on spore germination was considered by the writer in a series of experiments. Fresh spores of the fungus were brushed on glass slides and incubated in Petri dishes containing moist filter paper. One set of slides in each experiment was placed in a black light-proof box; another set received only daylight; and a third set was exposed throughout the total period of incubation to artificial light of a 60-Watt Mazda daylight lamp, but far enough from it to escape a lethal temperature influence. The details of the experiment and the results are presented in Table 4. Continuous darkness was more favorable for germination and growth than a combination of daylight and night darkness. Light definitely retarded and suppressed spore germination and growth.

Table 4. Effect of Light on Spore Germination and Growth in Length of Germ Tube

Experiment	Temperature °F.	Exposure Hours	Continuous Darkness		Day and Night		Continuous Light	
			Germination	Growth, Microns	Germination	Growth, Microns	Germination	Growth, Microns
1	60–70	24	Good	33.4	Poor	18.3	None	0
	60–70	48	Good	58.3	Poor	49.6	None	0
	60–70	72	Excellent	83.1	Fair	65.8	Trace	32
2	60	24	Good	19.9	Good	13.6	Poor	8.1
	60	48	Good	25.6	Good	22.3	Poor	14.7
3	60–70	57	Excellent	70	Fair	55	None	0
4	60–70	120	———	94	———	72	———	66
5	70	48	Good	72	Poor	49	Trace	26
6	60–70	24	Poor	32.6	Poor	35	None	0
Average				54.3		42.3		16.3

INFECTION PHENOMENA

Method of Infection

Infection of the foliage and the green floral structures is entirely through the stomata, and this manner of infection is believed to be due to a chemotactic stimulus within the stomata exerted upon the germ tube (11, 13). Stomata are present on both surfaces of the tomato leaf, but their numbers are much greater on the lower surface. According to Small (29, 30), infection may occur on either surface of the leaf, but inoculation of upper leaf surfaces produced leaf mold only on the lower surfaces. Makemson (13) obtained successful infections on both leaf surfaces but more on the lower surfaces. Caldis and Coons (5), using bits of mycelium from pure culture, succeeded in infecting leaves only by inoculations of the lower leaf surfaces.

In the writer's experience, the fungus always develops on the lower leaf surfaces first, but in the later and final stages of the disease the upper leaf surfaces also become densely covered with the fungus. Under natural conditions of inoculation the older terminal leaflets are always the first to become infected, but according

to Small (29), leaflets of various ages are equally susceptible, and this conclusion is substantiated by the writer's inoculation experiments. According to Makemson (13), the germ tube may immediately enter a stoma but usually considerable growth in length takes place before penetration. He noted cases of penetration 36 hours after inoculation. Williams (39) found that penetration had not occurred within 39 hours and concluded that a long period elapsed before penetration takes place. Hasper (11) observed that penetration usually required 4 to 8 days, while 10 to 12 days were required in other instances.

The writer's studies point to the importance of stomatal numbers and diameter in infection. It was observed that under greenhouse conditions the stomatal openings on the lower leaf surfaces are larger and the stomata much more numerous (11), and open over much longer periods each day of 24 hours, than on the upper leaf surfaces. The presence of infection only on the lower leaf surfaces in the beginning of epidemics is evidence of the significant relation of stomatal openings and numbers to infection. It has been asserted that plants in the open have fewer stomata than plants in the greenhouse (6) and that this is one factor accounting for the less frequent occurrence of the disease in the open. No differences in stomatal numbers were apparent from the writer's examinations of greenhouse and outdoor plants of the same variety.

Soil Moisture

Small (27, 31) noted that turgid plants become infected more readily than drooping plants, and observed that spores on drooping foliage failed to germinate. The higher humidity around turgid leaves permitted germination and infection. The belief prevails that artificial forcing conditions influenced by high temperatures, excessive moisture, and fertilization, greatly increase the susceptibility to disease, while more natural conditions in the open are less inducive to infection (14, 19). Volk (36) found no difference in the susceptibility of the leaves of plants growing in soils with moisture between 50 and 80% of the water-holding capacity. On wilting plants growing in a soil containing 25-30% moisture the incubation period was prolonged, fructifications were more abundant, and the viability of the fungus was extended.

Both turgid and wilting tomato plants were inoculated by the writer on August 16. On August 20 germination on the turgid foliage was considerable, the germ tubes were up to 80 microns in length, some capped with appressoria as noted by Makemson (13), and some tubes already lodged in the stomatal cavities. No branching of the tubes was evident. The tips of many of the tubes were lying directly over the closed stomatal cavities. In contrast to this condition, wilting plants inoculated at the same time and maintained in a wilting condition showed no evidence of spore germination by August 22, and when examined frequently the stomata on both leaf surfaces were tightly closed. On September 7 the foliage of the turgid and wilting plants was examined for infection (Table 5). The difference in the number of leaflets available for counting was due to the vast difference in growth associated with these extreme soil moisture conditions.

In another experiment the lower leaf surface of turgid and wilting plants grown in ground beds in the greenhouse was inoculated on August 18. Examinations of foliage 48 hours after inoculation revealed no spore germination on wilted plants growing in dry soil, but an abundance of it on turgid plants growing in moist soil in the same greenhouse; and the same condition existed on August 22. A deficiency of moisture sufficient to induce a flaccid condition of the leaf causes the

Table 5. Influence of Turgidity of Foliage on Infection

	Total Number of Leaflets	Infected Leaflets Percent
Turgid Plants		
1	111	23.4
2	84	33.3
3	84	33.3
Flaccid Plants		
1	63	0
2	46	0
3	52	0

closing of the stomata. The wilting plants were subsequently maintained under soil moisture conditions making for turgidity, and at the end of 48 hours considerable spore germination was noted. Next to light, the moisture supply of the leaves is the factor which most universally affects the opening or closing of the stomata. Turgidity, therefore, contributes to the conditions necessary for infection. Open stomata and respiration are definitely correlated with turgidity and give rise to a greater local humidity. The greater amount of tissue disorganization and fungus mycelium in the spongy parenchyma and about the tracheary tissue than in the palisade parenchyma in newly infected leaves suggests that conditions in the spongy parenchyma play a part in the preponderance of infection on the lower leaf surfaces.

Both Dyke (7) and Weiler (38) have noted that tomatoes are attacked by leaf mold in new houses more readily than in old houses. Dyke declared that tomatoes do not take the disease as readily under shaded as under clear glass, on the assumption that glass which allows more heat and light to pass is more favorable to the progress of the disease. According to the writer's observations, new greenhouses in locations outside of vegetable trucking areas are usually free of leaf mold for the first one or two years of growing, because of the absence of nearby sources of the fungus. In established trucking districts epidemics of leaf mold of equal severity have been noted on the first cropping of tomatoes in new and old greenhouses.

Bright sunlight is regarded as a lethal or unfavorable factor. It is reported that the disease develops earliest and best in parts of the house made hottest by the sun, corresponding to the south and west sides, and some reports appear to attribute this to light. Around Cleveland, Ohio, houses built north and south are reported to be freer of the disease than east and west houses (2) because in the former more sunlight is allowed to penetrate between the rows and temperature fluctuations from sunlight are less rapid and severe. Makemson (13) noted that dark, cloudy days furnished ideal conditions for the disease. Volk (36) found that tomatoes were more seriously diseased in darkness than in light. The toxic influence of light on fungous pathogenes of plants in greenhouse culture was recognized by Stone (34).

Since infection is obtained only under conditions which favor the opening of the stomata, light is an important factor for infection; and since the stomata close in darkness infection does not occur at night. Infection on the upper leaf

surfaces is handicapped by the lethal influence of strong sunlight on the fungus itself. Temperature and humidity operate more favorably for spore germination on the lower shaded leaf surfaces. When the sun is shining brightly, the temperature is obviously lower on this side of the leaf than on the upper surfaces, and the air is not as dry as that adjacent to the upper surfaces.

Conditions at the leaf surfaces are vital to the infection process. This is shown by the results of the writer's inoculations of upper and lower surfaces of leaflets with dry spores applied with a camel's-hair brush in mid-August in the greenhouse, at a time when warm temperatures and strong light conditions prevailed. No germination occurred on the upper lighted leaf surfaces but it was abundant on the lower shaded surfaces.

Langford (12) noted greater susceptibility to infection with less light and asserted that the genetic factor for resistance disappeared with the lack of light. The inherent resistance of the Stirling Castle tomato to one strain of *Cladosporium fulvum* was but slightly expressed during midwinter at Toronto, Canada, and accordingly varieties resistant during the summer season can be susceptible during midwinter. This has not been the case in the writer's experience, nor are any similar instances on record. Infection among susceptible varieties requires very specific conditions of host and environment. Variation in the occurrence of the disease closely follows differences in those fundamental environmental factors which influence stomatal movements and spore germination. Proper incubating conditions for infection are necessary to determine the true reaction of the variety. Varieties and hybrids of *Lycopersicum esculentum* reported to possess resistance have become badly diseased under conditions favorable for infection and have for that reason been abandoned as a source of resistance in this work. Even admitting the possibility of strains of the fungus, the conflicting reports asserting the type of reaction of "esculentum" tomatoes to *Cladosporium* cannot be taken too seriously. Susceptible varieties, including Stirling Castle, or hybrids of parents showing some resistance in the summer months have manifested little if any disease in midwinter in the greenhouse, and this is due to fundamental influences of temperature and relative humidity at the leaf surfaces, which are more favorable for the fungus at one season than at the other, and not to a host reaction that is genetically plastic to infection with changes in the light experience of the plants.

Nutrients

The relation of nutrients to the susceptibility of tomatoes to infection has been given considerable study abroad but there is no consistency in the results. Schaffnit and Volk (24, 25) and Volk (36) found that outstanding resistance was manifested by plants having deficient supplies of phosphoric acid or nitrogen, and that the lack of phosphoric acid devitalized the fungus sufficiently to render it less viable and infective. Superfluity of nitrogen, deficiency of potash, or excessive application of all the constituents rendered the plants very susceptible. Intermediate manifestations were shown when the plants were given normal quantities of all the constituents, or an excess of potash and phosphoric acid. Fleischmann (8) found that the development and extension of the parasite was greatly increased on overnourished plants and that deficiencies of important nutrients caused both weak plants and a check in the growth of the fungus. He found that acid phosphate and potash lacked the effect of increasing resistance, and that susceptibility and immunity are varietal manifestations which are not essentially influenced by

nutrition. Small (29) noted a severe development of leaf mold on manured plants, while on starved plants the infected leaf areas remained small and bore comparatively little of the fungus. Reusrath (20) cautioned against the use of excess or unbalanced nitrogen and advocated the liberal use of potash as a means of moderating the susceptibility of the tomato to disease. According to Rice (21) superphosphate has an encouraging effect, and potash and nitrogen a retarding influence.

These opinions cannot be taken too seriously in view of the fact that the chief objective of the grower is a high yield of quality fruit. Plant vigor is a prerequisite to success and obviously is obtained by proper fertilizer balance, soil moisture, temperature, and humidity. The opinions reported above are based largely on sand and peat cultures supplied with different ratios of potash, acid phosphate, and nitrogen; and the effect on yield and quality of the fruit appears to have been of minor consideration. Further, the tomato is susceptible to several physiological disorders such as blossom end rot, growth cracks, puffiness, hollow stem, blotchy ripening, greenback, edema, etc., which are associated with malnutriton, weather, and soil moisture. The suggestion of Volk (36) that more effort should be directed to provide environmental conditions which render the host less favorable to infection, rather than those which affect the activity or suppression of the parasite, disregards the resulting danger from other abnormalities which may prove more serious than leaf mold. Neither have conditions influencing weak or vigorous growth or the presence or absence of any of the abnormalities mentioned above shown under commercial conditions observed by the writer any apparent influence upon the susceptibility of tomato plants to leaf mold. The proper fertilizer amendments to the land, soil moisture, and temperature, to obtain plant vigor are vital to a successful yield, and any contrary practices employed as a means of counteracting a particular limiting disease factor are unwise.

Chemical or Induced Immunization

Efforts have been made to immunize the leaf tissues to infection by introducing chemical substances into the roots. In some experiments reported by Massee (14), tomato plants were immunized to Cladosporium by watering every three days from two to six weeks of age with a solution of copper sulfate (1-7000). After six weeks, the plants were watered every fourth day with a stronger solution (1-6000). None of the plants given the copper sulfate showed leaf mold.

Norton (18) used similar and weaker solutions of copper sulfate. Injury occurred except at a dilution of 1-10,000 but plants so treated developed Cladosporium in five days. The results from applying chemicals through stems or roots were in general negative. Hasper (11) also reported negative results. In view of these findings and the lack of practical application, no consideration has been given to this phase of the problem in this study.

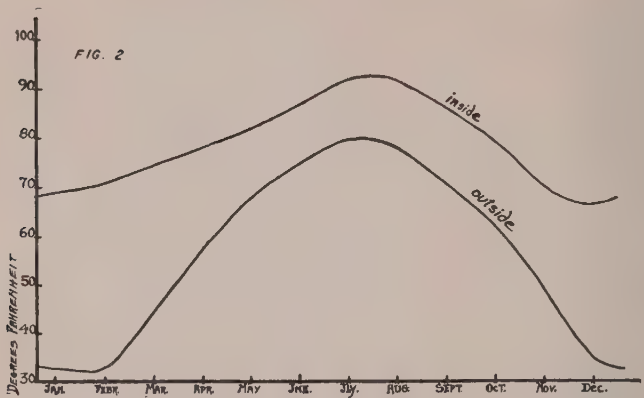
Relative Humidity and Temperature

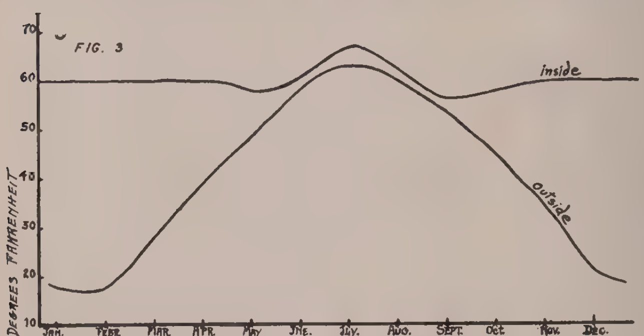
Volk (36) obtained the highest number of successful inoculations at 95% relative humidity. According to Bewley (4) and Small (26, 27, 28, 31), infection is slight or rare at an optimum growing temperature of 72° F. at 70-71% relative humidity, but severe at 80% and higher. At 58% and less despite an optimum growing temperature, or at temperatures less than 59° F. despite a favorable relative humidity, the fungus is suppressed or develops very slowly.

Rippel (22) declared that average relative humidities are insufficient for a proper analysis of the problem and that values less than 85% for 18 to 20 hours each day are necessary to check or prevent the disease. Walker and Sumner (37) declare that relative humidities around 80% and lower are against infection, while continuous exposure for 48 hours, or for a 2-hour period each day for 14 consecutive days, to relative humidities above 80% promotes infection. Alexander (2) found that very little infection occurs when plants are exposed for less than 9 hours in a saturated atmosphere at 59°-85° F. In clear weather, in early spring in Ohio, the greenhouse air is saturated usually less than 8 hours daily so that infection does not occur. From late spring to November, high humidities prevail for a long time and infection is epidemic. A significant concept is expressed by Newhall and Wilson (16) and Newhall (17) to the effect that relative humidities of 90-96% prevail at the leaves even though the greenhouse air may be as low as 75% and that this is due to leaf transpiration. The coincidence is noted of the disease being most severe when the transpiration rate is the highest or when the average house temperature is above 65°-70° F.

In greenhouse tomato culture in Massachusetts, the leaf mold disease appears in May, is epidemic during the summer months, and gradually subsides after October if the heating is properly managed. Bad attacks of the disease in August and September cause the fungus to persist throughout the autumn season especially if the weather is mild. The greenhouse mean maximum temperatures rise above 90° F. and prevail there from late June to mid-August, then recede to about 65° F. in December (Fig. 2). The outside mean maximum temperatures reach the highest (75°-80° F.) and the lowest (32°-34° F.) levels in the corresponding periods. The influence of high temperatures on leaf transpiration which supplies the moisture necessary for spore germination must be conceded. From May to October inclusive, pipe heating is either irregular or discontinued since greenhouse temperatures prevail above or close to the minimum temperatures for satisfactory growth (Fig. 3). This situation renders the prevention of high relative humidity in the greenhouse difficult if not impossible during this critical period, even with ventilation. After this period, beginning with October, the increasing gap between the inside and outside temperatures, reaching a maximum of almost 45° F., effects a corresponding decrease in the mean relative humidity which is at the lowest level in the months of December, January, and February, corresponding to the widest differences in temperatures. As the season advances, the gap between the outside and inside mean minimum temperatures becomes extremely narrow, being the smallest, or less than 5° F., from June to September inclusive. This temperature differential, directly as it affects the relative humidity, is a major influencing factor governing the behavior and progress of the disease in the greenhouse. The usual failure of the fungus to sporulate on the leaf surface in the winter months is due to the prevailing low relative humidity (27, 36).

The average mean and mean maximum relative humidity under glass are shown graphically in Fig. 4. These reach peak levels from May to September inclusive, corresponding to the highest monthly mean temperatures. During this period the average mean relative humidity inside is about 80-82%, and the mean maximum 100%. At the leaf surface, due to a high transpiration rate under these conditions, the relative humidity is usually near, or at, 100%. The more abundant application of water to the soil in the warmer months, and its influence on the humidity of the greenhouse air, must also be recognized. Since temperatures of 74°-79° F. and relative humidities of 98-100% are optimum for spore germination and infec-





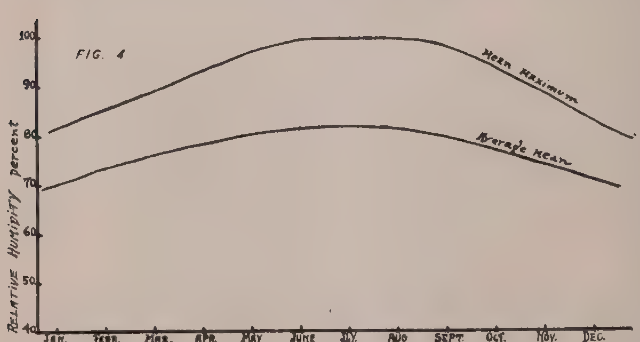


Figure 2. Approximate Course of Monthly Mean Maximum Temperature in Tomato Culture under Glass and in the Open in Massachusetts

Figure 3. Approximate Course of Monthly Mean Minimum Temperature in Tomato Culture under Glass and in the Open in Massachusetts

Figure 4. Approximate Course of Monthly Mean Relative Humidity in Tomato Culture under Glass in Massachusetts

tion, it is obvious that at this season ideal temperature and moisture conditions for the fungus prevail.

A clearer understanding of temperature and humidity conditions prevailing under glass in the culture of tomatoes in Massachusetts may be obtained from a study of some of the weekly record charts. Under summer weather conditions day temperatures often reach 95° F. and higher, in spite of ventilation, and the minimum temperature is hardly ever below 60° F. A peak relative humidity of 100% prevails almost every night (Fig. 5-A). In bright weather and with ventilation, the relative humidity values in the greenhouse recede with rising temperatures, and the lowest relative humidity values are associated with the highest air temperatures. These are the conditions of the air some distance from the leaf itself. At the leaf surface higher humidity prevails. The records of temperature and relative humidity outside the greenhouse for the week ending September 30, 1929, show the same wide fluctuations in night and day conditions (Fig. 5-B). Moisture saturation with the lowest temperatures prevails at night, and the lowest relative humidities (below 50%) with the highest temperatures occur at midday. It is evident, as Rippel (22) noted in Germany, that the relative humidity in the greenhouse is above 80% for much of the day, and only for a short time under 60% in the off or mild heating season.

With the beginning of the boiler heating season in September and October, some influence of heat on the humidity of the greenhouse air (Monday and Tuesday, Fig. 6-A) is shown; while lacking heat (Wednesday to Sunday) a relative humidity of 100% prevails regularly in spite of ventilation. At this season, the temperature difference between the inside and outside air is so small, or zero, that there is usually little if any effect from boiler heat on the humidity of the greenhouse air, even when supplemented with ventilation, unless the temperature is raised unreasonably high. The influence of heat on the humidity of the air is thus clearly demonstrated in Fig. 6-A, 6-B, and 7-B.

During cold winter weather and with the greenhouse temperatures maintained at and near 60° F., the wide fluctuations of temperature and humidity prevailing during the warmer months are smoothed off to rather narrow limits (Fig. 7-A and 7-B) except when periods of warm weather interrupt to cause the outside temperature to converge closely upon the minimum inside growing temperature. These periods introduce high relative humidities which may be controlled by proportionately higher temperatures. The need for ventilation supplementary to heat at these times is significant.

To obtain more intimate knowledge of the problem, frequent readings of the Mason hygrometer and psychrometer were made in different locations in the greenhouse at, and away from, the foliage and with different outside weather conditions and amounts of ventilation. A set of readings was taken on a rainy day in April when the outside temperatures were 42° to 52° F. and the relative humidity 100%. A rotary fan was operated 6½ feet from the ground and in the center of a greenhouse of 10,000 cubic feet (Table 6). Without ventilation and with the particular outside conditions prevailing when these readings were taken, the relative humidity at the foliage was 100%; at the ground between the rows of plants 83 to 88%; and at the fan 83 to 88%. Inside temperatures were in the range of 60° to 70° F. In these instances, the air re-circulated by fanning lacked sufficient evaporating power to influence the relative humidity at the foliage. Obviously, the greenhouse air must be changed with much drier outside air, or diffused with much colder outside air and heated, to obtain an appreciable reduction of the relative humidity.

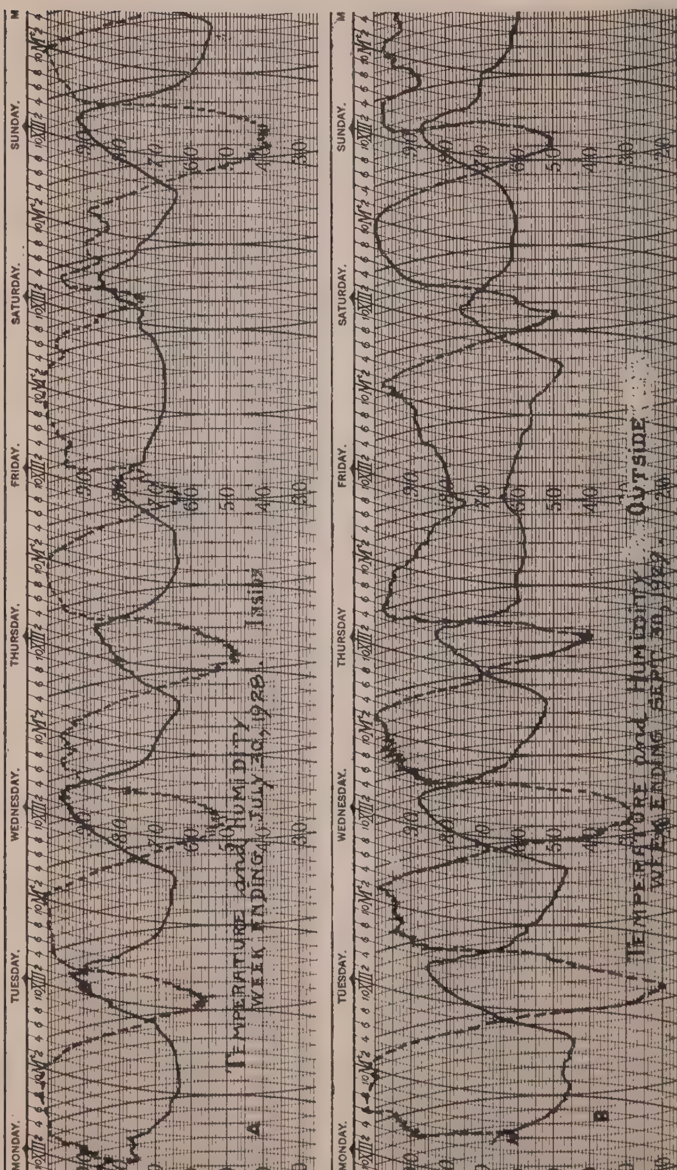


Figure 5. Instrument Records of Temperature and Humidity
A, in the greenhouse; B, outside the greenhouse
Temperature ——— Relative Humidity - - - - -

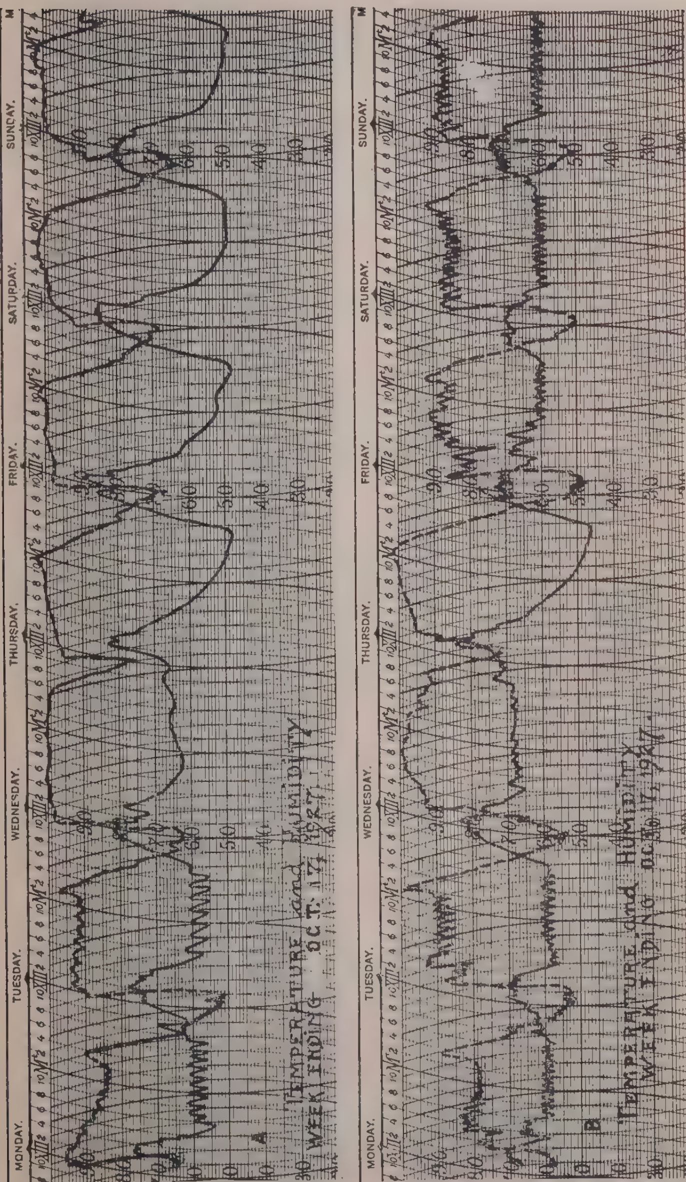


Figure 6. Instrument Records of Temperature and Humidity in Two Separate Greenhouses
Temperature ——— Relative Humidity - - - -

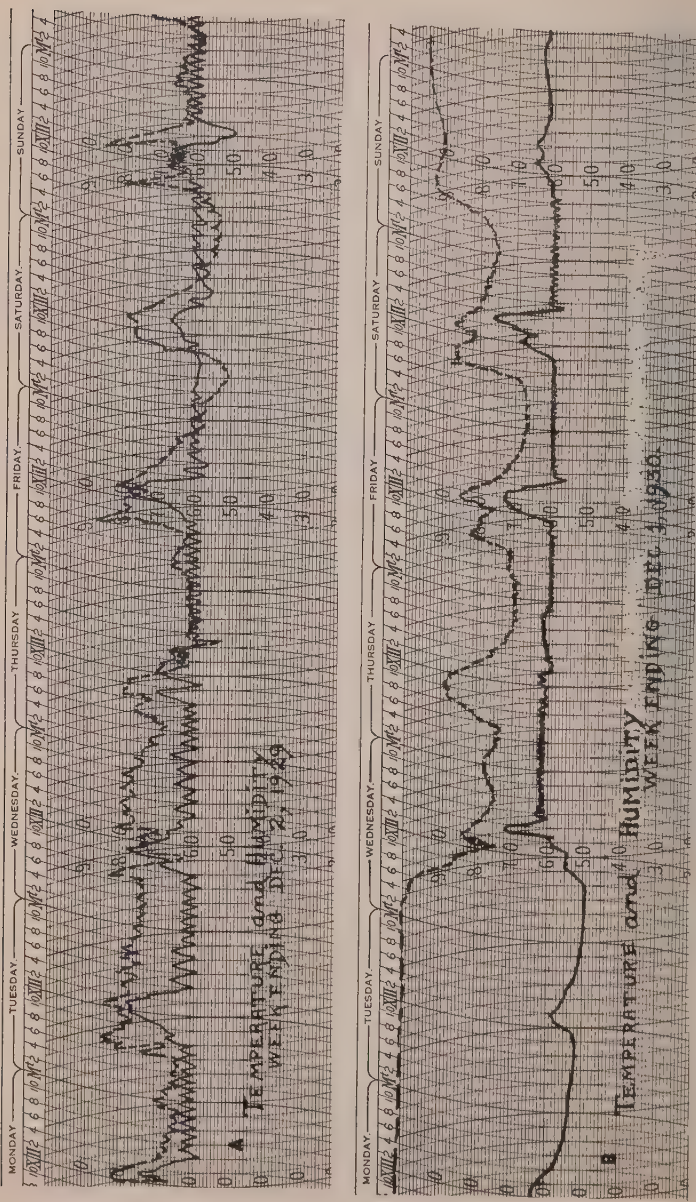


Figure 7. Instrument Records of Temperature and Humidity in the Greenhouse
Temperature ——— Relative Humidity - - - - - -

TABLE 6.--TEMPERATURE AND RELATIVE HUMIDITY IN GREENHOUSE PLANTED TO TOMATOES

(Readings on rainy day in April, 1929: outside relative humidity, 100 percent)

Air Temperature °F.	Relative Humidity Percent	Hour	Position of Hygrometer
64	82	8:45 a.m.	In corner near plants
65	83	8:45 a.m.	At fan
64	88	9:00 a.m.	In corner near ground
67	88	9:00 a.m.	At fan
64	88	9:00 am..	Between rows near ground
68	100	9:30 a.m.	At foliage
69	83	9:30 a.m.	At fan
70	88	10:00 a.m.	Between rows 8 inches from ground
70	83	10:00 a.m.	At fan
69	100	10:30 a.m.	At foliage
70	83	10:30 a.m.	At fan
70	88	11:00 a.m.	In draft halfway between fan and ground
70	88	11:00 a.m.	Between rows 8 inches from ground
68	100	11:00 a.m.	At foliage
69	83	11:00 a.m.	At fan

This is substantiated further by another set of readings (Table 7) obtained during rainy weather and when the greenhouse atmosphere was stirred by ventilation rather than by the motions of an electric fan. As the readings reveal, the influence of ventilation during wet weather conditions outside on the relative humidity inside is quite insignificant in the absence of heat. Under these conditions, the air at the leaf surface is saturated with moisture.

TABLE 7.--TEMPERATURE AND RELATIVE HUMIDITY IN GREENHOUSE PLANTED TO TOMATOES

(Readings in moist, cloudy weather)

Ventilation	Hour	Away from Foliage		At Foliage	
		Air Temperature °F.	Relative Humidity Percent	Air Temperature °F.	Relative Humidity Percent
All ventilators and doors open	4:00 p.m.	68	88	66	100
All ventilators open .	2:00 p.m.	62	100	61	100
All ventilators and doors open	8:00 p.m.	64	94	63	100
Top ventilators open	9:00 a.m.	62	100	61	100
Top ventilators open	2:00 p.m.	71	88	70	100

In contrast to the previous tests, readings were taken under prevailing bright weather conditions in May, October, and November (Table 8) when ventilation was provided from the top and sides of the greenhouse. These readings show higher relative humidities and lower temperatures at the foliage than in the open atmosphere between the rows of plants. The introduction of drier outside air by ventilation reduces the relative humidity at the foliage, and the reduction is greatest when both the top and side ventilators are opened. Previously it was shown that saturated moisture conditions prevail at night during the warmer months. It is also evident that relative humidities above 95%, accompanied by optimum temperatures for the fungus at the leaf surfaces in consequence of high rates of transpiration, are of common occurrence during the day throughout the warmer months in spite of ventilation.

TABLE 8. TEMPERATURE AND RELATIVE HUMIDITY IN GREENHOUSE PLANTED TO TOMATOES

(Readings in bright weather in May, October and November. Ventilators Open.)

Away from Foliage		At Foliage	
Air Temperature °F.	Relative Humidity Percent	Air Temperature °F.	Relative Humidity Percent
61	74.5	58.5	96.5
62.5	80	62	94
66	83	63	97
67	73	63	91
71	73	70.5	97
71	78	68.5	91
83	64	74	89
85	61	80	85
84	72	80	85
87	65	83	100
88	61	84	85
89	73	82	98
90	62	84	85
94	60	90	81

Newhall and Wilson (16) and Newhall (17) asserted that with rapid air changes a relative humidity as high as 90% in the greenhouse may exist without infection. With infrequent air changes a relative humidity as low as 60% would be required to prevent infection. They noted that in a stagnant atmosphere infection proceeds when the greenhouse air is as low as 80% relative humidity. The writer's readings reveal that the recirculation of air of high relative humidity and of nearly similar temperature does not influence humidity conditions at the leaf surface and has little effect on the humidity of the air itself. The infiltration of cold outside air and warming it to maintain a minimum growing temperature of about 60° F. produces a drying greenhouse atmosphere and this condition is most pronounced in the coldest months of the year. In the warmest months of the year the introduction

and free circulation of outside air of real low relative humidity produces the greatest evaporating effect at the leaf surface. Between these extremes of maximum heating in the winter and maximum evaporation from ventilation in the driest summer weather, favorable conditions for infection commonly occur in the greenhouse which, even in spite of heat or natural and forced ventilation or both, and within the limits of good plant growth, are often beyond any reasonable or practical means to counteract.

Small (26) noted the most progressive development of the disease in July and August, the warmest months, in England and when air saturation occurred in the houses at night. The evidence fully substantiates the view that seasonal variations in the severity of leaf mold are related fundamentally to temperature (16, 17, 27), other conditions being favorable for good growth of the tomato plant.

SUMMARY

In greenhouse tomato culture in Massachusetts, the leaf mold disease is usually epidemic from June to October. It occurs in field plantings near greenhouses and in areas of uneven or sheltered topography and poor atmospheric drainage. The fungus is a facultative parasite.

Only the conidial stage of the fungus is known. The spores withstand severe winters and remain viable under the most adverse conditions for 9 to 12 months. Conidia are disseminated by air currents and are readily dislodged by shaking or disturbing the plants.

A relative humidity of 100% or precipitated moisture and temperatures of 75°-78° F. are optimum for germination. A relative humidity of 95-96% is minimum and 40° F. and 94° F. are the minimum and maximum temperatures for spore germination. Conidia lose their viability when exposed to a temperature of 115°-116° F. for 2 hours. Longer exposures at slightly lower temperatures are also lethal. The exposure of infected plants for 3 hours to 118°-123° F. does not affect germination of the fungus appreciably and is injurious to the tomato plant.

Light retards growth and suppresses spore germination. Strong light is lethal to the spores.

Infection is through the stomata, usually or entirely in the lower sides of the leaves where the stomata are most numerous and where conditions within the leaf and light, temperature, and relative humidity at the leaf surface operate more favorably for spore germination than at the upper leaf surfaces.

Open stomata and transpiration are associated with light and turgid growth. Flaccidity of the foliage, brought on by a moisture deficiency in the leaves, and darkness operate to close the stomata and to hinder infection.

Conditions at the leaf surface are fundamental to the infection process, and variations in the occurrence of the disease in the greenhouse at different times of the year are due to fundamental environmental factors operating to favor or prevent spore germination on the leaf.

Plant vigor is a necessary asset to high yields and quality, and the result of good growing conditions. Efforts at modifying the nutrition of the plant to influence the reaction of the host in the direction of resistance are not practical or commercially successful. Immunization of the host with chemical solutions applied to the soil has not proved safe or successful.

The disease is epidemic during the warmer months from June to October inclusive, when maximum greenhouse temperatures of 80° to 92° F. prevail; when

the mean minimum inside and outside temperatures converge to a narrow difference of less than 5° F.; and when the highest mean maximum relative humidity of 94-100% for the year prevails. The influence of high temperature on leaf transpiration and infection is recognized. The severity of the disease is related fundamentally to temperature.

LITERATURE CITED

1. Anon. Fungi injurious to tomatoes. Jour. Bd. of Agr. (London) 5:192-197. 1898.
2. Alexander, L. J. Tomato leaf mold and greenhouse ventilation. Proc. Ohio Veg. Growers Assoc. 16:87-91. 1931.
3. Bancroft, C. K. Relationship between Cladosporium and Hormodendron. Ann. Bot. (London) 24:359-372. 1910.
4. Bewley, W. F. Tomato leaf-mould disease. Min. Agr. and Fish. (Great Britain) Leaflet 262, 1-6, 1929.
5. Caldis, P. D. and Coons, G. H. Achromatic variations in pathogenic fungi. Papers Mich. Acad. Sci., Arts, and Letters. 6:189-236. 1926.
6. Chamberlain, E. E. Tomato leaf mold (*Cladosporium fulvum*). New Zeal. Jour. Agr. 45, No. 3:136-142. 1932.
7. Dyke, W. Tomato mildew. The A B C of tomato culture under glass. Lockwood Press, London, 1925. Lit. cit. pp. 116-123.
8. Fleischmann, C. Die Widerstandsfähigkeit verschieden ernährter Pflanzen gegen parasitäre Krankheiten. Gartenwelt 31, No. 52:785-786. Dec. 30, 1927.
9. Gardner, M. W. Potato and tomato diseases. Trans. Ind. Hort. Soc. 64, 1924:125-132. 1925. Lit. cit. pp. 130-131.
10. ———— Cladosporium leaf mold of tomato; fruit invasion and seed transmission. Jour. Agr. Research 31:519-540. 1925.
11. Hasper, E. Biologie und Bekampfung des Cladosporium fulvum Cke. auf Solanum lycopersicum. Zeitschr. Pflanzenkrank. 35:112-118. 1925.
12. Langford, A. N. The parasitism of Cladosporium fulvum Cke. and the genetics of resistance to it. Canad. Jour. Research (Sec. C) 15, No. 3: 108-128. 1937.
13. Makemson, W. K. The leaf mold disease of tomatoes caused by Cladosporium fulvum Cke. Mich. Acad. Sci. Ann. Rept. 20, 1918:316-348. 1919.
14. Massee, G. On a method for rendering cucumber and tomato plants immune against fungous parasites. Jour. Roy. Hort. Soc. 28:142. 1903.
15. Newhall, A. G. and Wilson, J. D. A preliminary report on forced air ventilation for the control of Cladosporium leaf mold of greenhouse tomatoes. Phytopath. 19:83. 1929.
16. ———— and Wilson, J. D. Humidity and control of leaf diseases in greenhouses. Ohio Agr. Expt. Sta. Ann. Rept. 47, 1927-1928. Bul. 431:64-65. 1929.
17. Newhall, A. G. The relation of humidity and ventilation to the leaf mold disease of tomatoes. Ohio Agr. Expt. Sta. Bi-Month. Bul. 132, Vol. 13, No. 3:119-122. 1928.

18. Norton, J. B. S. Internal action of chemicals on resistance of tomatoes to leaf diseases. Md. Agr. Expt. Sta. Bul. 192:17-30. 1916.

19. Parker, T. The suppression of insect pests and fungoid diseases. Bur. Biotechnol., Leeds (England) Bul. 10, Vol. 2:68-72. 1923.

20. Reusrath, Th. Betrachtungen über die Braunfleckenkrankheit der Tomaten. Gartenwelt 35, No. 26:354. 1931. Also same text in Möller's Deut. Gärt. Zeit. 46, No. 28:335, 1931, with title Die Verhütung der Braunfleckenkrankheit der Tomaten.

21. Rice, W. H. Control of tomato mildew. New Zeal. Jour. Agr. 36:99-102. 1928.

22. Rippel, K. Untersuchungen über die Abhangigkeit der Sporenkeimung vom Wassergehalt der Luft bei Cladosporium fulvum Cke. und anderen Pilzen. Arch. f. Mikrobiol. 4:530-542. 1933.

23. Salmon, E. S. and Ware, W. M. Report of Department of Mycology 1934-1935. Jour. South-Eastern Agricultural College, Wye, Kent (England) No. 37:17-18. Jan. 1936.

24. Schaffnit E. and Volk A. Über den Einfluss der Ernährung auf die Empfänglichkeit der Pflanzen für Parasiten (I Teil). Forsch. auf dem Gebiet der Pflanzenkrankh. u. der Immunität im Pflanzenreich 3:1-45. 1927.

25. ———— and Volk, A. Beiträge zur Kenntnis der Wechselbeziehungen zwischen Kulturpflanzen, ihren Parasiten und der Umwelt. (II Mitteilung.) Über den Einfluss der Ernährung auf die Empfänglichkeit der Pflanzen für Parasiten (II. Teil). Phytopath. Zeitschr. 1:535-574. 1930.

26. Small, T. Tomato leaf mould. Expt. and Research Sta., Cheshunt, Herts, Ann. Rept. 13 (1927):46-51. 1928.

27. ———— Tomato mildew or leaf mould. Ibid. 14 (1928):45-62. 1929.

28. ———— Temperature and humidity in relation to tomato mildew (Cladosporium fulvum). Ann. Appl. Biol. 16:192. 1929.

29. ———— Tomato leaf mould. Expt. and Research Sta., Cheshunt, Herts, Ann. Rept. 15 (1929):43-51. 1930.

30. ———— Tomato leaf mould. Ibid. 16 (1930):40-56. 1931.

31. ———— The relation of atmospheric temperature and humidity to tomato leaf mould (Cladosporium fulvum). Ann. Appl. Biol. 17:71-80. 1930.

32. Spangler, R. C. Cladosporium fulvum. Bot. Gaz. 78:349-352. 1924.

33. Stair, E. C., Brown, H. D., and Hienton, T. E. Forced ventilation as a means of controlling tomato Cladosporium and Septoria in hotbeds. Phytopath. 18:1027-1028. 1928.

34. Stone, G. E. The relation of light to greenhouse culture. The relation of light to pathological conditions. Mass. Agr. Expt. Sta. Bul. 144, 1913. Lit. cit. p. 5-6.

35. Thompson, R. Yellow spot (Cladosporium fulvum). The Gardener's Assistant n. ed. II:340-341. 1904.

36. Volk, A. Beiträge zur Kenntnis der Wechselbeziehungen zwischen Kulturpflanzen, ihren Parasiten und der Umwelt. (IV Mitteilung). Einflüsse des Bodens, der Luft und des Lichtes auf die Empfänglichkeit der Pflanzen für Krankheiten. Phytopath. Zeitschr. 3:1-88. 1931.

37. Walker, J. C., and Sumner, C. B. Prevent tomato leaf mold by lowering greenhouse humidity. Wis. Agr. Expt. Sta. Ann. Rept. 1930-1931. Bul. 421:66-67. 1932.

38. Weiler, ———. Über Verhütung der Braunfleckenkrankheit der Tomaten. Möller's Deut. Gärt. Zeit. 46:392-393. 1931.

39. Williams, P. H. Tomato leaf mould. Expt. and Research Sta., Cheshunt, Herts, Ann. Rept. 11 (1925):67-72. 1926.

40. Wilson, J. D., and Alexander, L. J. Effect of greenhouse construction and management on the development of tomato leaf mold. Ohio Agr. Expt. Sta. Ann. Rept. 49, Bul. 470:60. 1931.

41. Wollenweber, H. W. Tomatenkrankheit und ihre Abwehr. Flugblatt. Biol. Reichsanst. f. Land-u Forstwirtschaft No. 118/119. 6 p. March 1932.

42. Wright, W. P. Tomato diseases. Cassell's Dictionary of Practical Gardening, 2:396, 1902.

Publication of this Document Approved by Commission on Administration and Finance
3500-7-'38. No. 4521.